Life history of harbor porpoises (*Phocoena phocoena*) in Scottish (UK) waters

J. A. LEARMONTH
School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen, AB24 2TZ, United Kingdom
S. MURPHY
Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, United Kingdom
and
Sea Mammal Research Unit, Scottish Oceans Institute, University of St Andrews, St Andrews, Fife, KY16 8LB, United Kingdom
P. L. LUQUE
School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen, AB24 2TZ, United Kingdom
R. J. REID, I.A.P. PATTERSON, A. BROWNLOW, H.M. ROSS, J. BARLEY
Wildlife Unit, SAC Veterinary Services, Drummondhill, Stratherrick Road, Inverness, IV2 4JZ, United Kingdom
M.B. SANTOS
Instituto Español de Oceanografía, Centro Oceanográfico de Vigo, P.O. Box 1552, 36200, Vigo, Spain
and
Oceanlab, Institute of Biological and Environmental Sciences, University of Aberdeen, Main Street, Newburgh, Aberdeenshire AB41 6AA, United Kingdom
G. J. PIERCE
Oceanlab, Institute of Biological and Environmental Sciences, University of Aberdeen, Main Street, Newburgh, Aberdeenshire AB41 6AA, United Kingdom
and
CESAM & Departamento de Biologia, Universidade de Aveiro
3810-193 Aveiro, Portugal
E-mail: g.j.pierce@abdn.ac.uk

ABSTRACT

Life history parameters were determined for stranded and bycaught harbor porpoises (*Phocoena phocoena*) from Scottish (UK) waters (1992-2005). Fetal growth rate was 84.4 mm/mo and mean size at birth was 76.4 cm (range 65-88 cm). Males and females had a similar range of body lengths (65-170 cm and 66-173 cm, respectively), although asymptotic lengths were higher in females than males (approximately 158 cm and 147 cm respectively). Nonpregnant females were significantly lighter, in relation to their length than males. Maximum estimated age was 20 yr for both sexes. Age at sexual maturity (ASM) was estimated as 4.35 yr in females and 5.00 yr in males. Conception occurred mainly in July and August although reproductively active males were recorded during April to July. Gestation lasted 10-11 mo, with calving mainly between May and July. Lactating females were recorded during June to November, while small calves with solid food in their stomachs were found mainly during February to May. Estimated pregnancy rate (0.34 to 0.40) is lower than recorded elsewhere, but is likely underestimated due to the prevalence of mature females of poor health status in the sample. Nevertheless, cetacean strandings can be an essential source of data on demographic parameters.

INTRODUCTION

The harbor porpoise (*Phocoena phocoena*) is the most abundant cetacean species in European Atlantic shelf waters (Evans 1980*;* Hammond *et al*. 2002*,* 2013; Reid *et al*. 2003). However, its general biology and ecology are poorly documented for many populations and stocks (Read *et al*. 1997*;* Haug *et al*. 2003). Few areas of biological research relate so directly to species conservation status as studies of life history, which includes examination of traits directly influencing fecundity, survival, and population growth. In marine mammals, age at sexual maturity (ASM), pregnancy rate and juvenile survival are the three parameters most likely to reflect changes in population status (Eberhardt and Siniff 1977*;* DeMaster 1984*,* Fowler 1984).

Harbor porpoises are subjected to various threats and pressures, including fisheries interactions, pollutants, disease, fatal attacks from bottlenose dolphins (*Tursiops truncatus*), and changes in prey availability (*e.g.*, Ross and Wilson 1996; Foster *et al*. 1999; Jepson *et al*. 2005; MacLeod *et al*. 2007; Pierce *et al*. 2008; Murphy *et al*. 2010; ASCOBANS 2011; Heide-Jørgensen *et al*. 2011). Concern for the species' status led to the Agreement on the Conservation of Small Cetaceans of the Baltic and North Sea (ASCOBANS) and the designation of Special Areas of Conservation for this species is required under the European Community (EC) Directive 92/43/EEC on the Conservation of Natural Habitats and of Wild Flora and Fauna (the Habitats Directive). In order to assess the potential effects of these threats on population status, it is important to determine and monitor life history parameters, such as ASM, pregnancy rates, and the timing of the reproductive season, along with information such as distribution, abundance and seasonal movement patterns (Stenson 2003).

Data from stranded and bycaught animals, despite some biases and limitations, remain the main (and often only) source of life history information for many populations, as a result of the

difficulties involved in observing and studying harbor porpoises in the wild (Palka 1996; Hammond *et al*. 2002) or keeping them in captivity (Kastelein *et al*. 1997).

The present study uses samples and postmortem information collected from stranded and bycaught harbor porpoises around Scotland over a 14-year period (1992-2005) to examine biological, reproductive and life history parameters. Porpoises were collected throughout the year and represented the full range of age and reproductive status classes for both males and females.

MATERIALS AND METHODS

The Scottish Agricultural College (SAC) Veterinary Services Division at Inverness conduct necropsies on stranded and bycaught cetaceans in Scotland as part of an ongoing DEFRA-funded monitoring and research program. Nine hundred and forty four stranded and bycaught harbor porpoises were recorded by the SAC around Scotland between 1992 and 2005. Necropsy, sampling and data collection procedures follow the recommendations of Kuiken and Hartmann (1991) and Law (1994). Data collected included location and date found for all animals. Necropsies were carried out on 545 animals, this lower figure reflecting both logistic constraints (*e.g*., funding) and the poor state of preservation of many carcasses. During necropsy, sex, total body length (cm), and mass (to the nearest 0.5 kg) were recorded. Cause of death was determined when possible. Where available, samples of teeth were collected for age estimation and reproductive organs to determine reproductive status. Stomach contents were collected for diet analysis (diet results to May 2005 were published in Santos *et al.* 2004).

Age determination

95 During postmortem examination, teeth were removed from the middle of the lower jaw and
96 preserved in 10% neutral buffered formalin. Tooth preparation methods were adapted from Hohn
97 and Lockyer (1995) and Lockyer (1995*b*). Teeth were cleaned and decalcified using a
98 commercial decalcifying agent (RDO©), prior to sectioning at 23-25 μm thickness in a freezing
99 microtome (-10°C). One tooth from each individual was sectioned parallel to the mandible
100 (porpoise cut) and the second was cut perpendicular to the mandible (dolphin cut). Both cuts
101 were made to ensure the optimum sections were obtained. The best sections (those that included
102 the crown of the tooth and the maximum area of pulp cavity) were selected for each tooth, stained
103 with either toluidine blue or Ehrlich's hematoxylin, and 'blued' in a weak alkaline solution. Two
104 stains were used, on duplicate sections, to maximize the likelihood that an accurate age could be
105 determined for each tooth. Stained sections were permanently mounted on slides using DPX
106 (BHL Laboratory Supplies, Poole, UK).
107 Age was estimated by examining the stained tooth sections using a binocular microscope
108 (x10-50 magnification) and counting the growth layer groups (GLGs), which are thought to be
109 laid down annually in odontocetes (Perrin and Myrick 1980). All estimates were initially made
110 'blind' (with no biological information on the animal) and replicate counts were made by at least
111 two experienced readers. If readers disagreed on the age of the animal, the sections were
112 examined again. If the difference was greater than one GLG, both readers re-read the tooth, and if
113 no agreement was reached another tooth from the same animal was sectioned and read by both
114 readers. Where possible, age was estimated to the nearest 0.25 yr interval for animals aged 2 yr or
115 less, to the nearest 0.5 yr interval for animals aged 3-4 yr, and to the nearest year for animals
116 aged over 5 yr. Note, however, that this was not always possible.

117 The animals for which teeth were not collected for age determination included 15 neonates
118 (≤90 cm). These animals were used in analysis of growth rate and to estimate average length of
119 neonates, although not for analysis of size and age at maturity.
120
121 *Fetal growth rate and size of neonates*
122 Fetuses were measured during the necropsy of pregnant females. Following examination of a
123 plot of fetal length against date, a linear regression was fitted to estimate the fetal growth rate
124 (see Huggett and Widdas 1951; Read 1990*b*), treating September, the month in which the
125 smallest fetus was recorded, as the starting point. Since the regression slope was in $mm.d^{-1}$, the
126 value was multiplied by 30.5 to give a monthly rate.
127 Amongst the smallest stranded animals, all those with length greater than or equal to the
128 smallest animal confirmed not to be an aborted fetus (65 cm) and less than or equal to 90 cm
129 were classed as "neonates" following Lockyer (1995*a*). Note however that, since these may
130 include animals up to around 2 months old, their estimated average length will not be the same as
131 size at birth. Recent births (n=8) were identified by the presence of hairs in bristle pits on the
132 rostrum, fetal folds, and/or dorsal fins that were not yet fully erect (Wilkin *et al.* 2012). We
133 followed the approach of Borgesson and Read (2003) in combining these data with data on those
134 fetuses which were larger than the smallest neonate (n=6; five were obtained from dystocia (or
135 dystokia, *i.e.*, difficult or abnormal birth) cases) to estimate length and mass at birth.
136
137 *Growth: length at age*
138 Gaussian GAMs were fitted to determine whether sex had a significant effect on the
139 relationship between body length (cm) and age. Preliminary analysis indicated no significant
140 effects of month or year so these variables were not included in the subsequent models. A model

with separate smoothers for the effect of age for each sex was compared (using ANOVA) with a model that used a common age-smoother for both sexes. The maximum number of knots (*k*) for the age smoother was set to 4 to avoid overfitting (*i.e.*, avoiding biologically unrealistically complex smoothing curves). The initial model was thus:

$$(Y1) \sim a + s(age, k=4, by=as.factor(Sex)) + factor(sex) + ei$$

where, *Y1* is body length, *a* is the intercept, s(*age*) is a smooth function of age and *ei* is the residual (unexplained information or noise, $ei \sim N(0, s2)$). Model validation included checking that residuals were approximately normally distributed, homoscedastic and contained no obvious patterns, and checking "hat" values to ensure there were no serious outliers. Separate models were fitted for each sex to derive approximate 95% confidence limits for the visually identified asymptotic size (since GAM does not fit a formula it is not possible to precisely locate the age at which asymptotic size is achieved). Models were fitted using the "gam" function from the mgvc library in R 2.9.1. Predicted lengths at each age and associated 95% confidence limits were then calculated using the "predict", "boot" and "boot.ci" functions in R 2.9.1.

Growth: mass at length

To quantify the length-mass relationship and test for differences between the sexes, we fitted Gaussian GAMs, with mass as the response and length and sex as explanatory variables. Length and mass were first log-transformed. For the length effect, *k* was set to a maximum of 4 to avoid overfitting. Models with separate smoothers for the effect of length for each sex were compared, using ANOVA, with models that used a common length smoother for both sexes. Finally the analysis was repeated excluding pregnant females. These analyses were carried out in Brodgar 2.7.1.

165 *Gompertz growth models*

166 Gompertz growth curves (Laird 1966, Fitzhugh 1975) were used to describe the growth
167 pattern and to predict length and age at physical maturity, separately for male and female harbor
168 porpoises, by using a three-parameter model in which the first parameter is length at birth (an
169 alternative formulation uses asymptotic length). The form of the Gompertz model used was:

170 $$L = L_0 \times e^{\left(a \times \left(1 - e^{(-b \times Age)}\right)\right)}$$

171 where, L_0 = birth length, a is the specific rate of exponential growth, and b is the rate of decay
172 of exponential growth. Although an independent estimate of L_0 was available from the present
173 study (see above), it was based on a small sample size and, in addition, not all ages of the
174 youngest animals could be estimated to the nearest 0.25 yr. Therefore we allowed the values of
175 all three parameters to be determined by the model. Exploration of two-stage Gompertz models
176 indicated that they offered no improvement of goodness of fit.

177 Equations were initially fitted using the nonlinear regression function in SPSS Version 20,
178 which provides parameter estimates (with 95% confidence limits) and a value for r^2. To generate
179 95% confidence limits for the fitted curve we re-ran the models in R (version 2.9.1) using the
180 "nls" command and bootstrapped the 95% confidence limits using the "boot" and "boot.ci"
181 commands (boot library).

182 In principle, individuals may be considered physically mature if they have a total body length
183 (TBL) equal or greater than the asymptotic value generated by the Gompertz equations. In
184 practice, since approach to an asymptote was slow we regarded the asymptote having been
185 reached once the 95% confidence limits of predicted length encompassed the predicted length at
186 20 yr old (the oldest animals available in this data set). To provide further evidence on asymptotic
187 size we also fitted a simple two-stage linear model, such that the first part had a positive slope

188 and the second part had a zero slope, and identified the switching point that minimized the sum of
189 squares.
190
191 *Female reproductive status*
192 During the postmortem examination of females, both ovaries were removed and preserved in
193 10% neutral buffered formalin, and any evidence of lactation or presence of a fetus was recorded.
194 If a fetus was present, it was weighed, sexed if possible, and measured.
195 Both ovaries were examined externally and internally to record the presence and number of
196 *corpora lutea* (CL) and *corpora albicantia* (CA) on the left and right ovaries. Assessment of
197 female reproductive status was based on procedures and terminology recommended by the
198 International Whaling Commission (Perrin *et al*. 1984) and used in similar studies (*e.g*., Read
199 1990*a,* Murphy *et al*. 2009). Females were considered sexually mature if the ovaries contained at
200 least one *corpus luteum* or *albicans*, and as immature if no *corpora* were present. Mature females
201 were assigned to one of the following classes: (a) Pregnant, based on the visible presence of a
202 fetus, but not lactating, based on the absence of milk in the mammary glands, (b) Pregnant and
203 lactating, (c) Lactating but not (visibly) pregnant, or (d) Mature but neither (visibly) pregnant nor
204 lactating (*corpora* were present in the ovaries, providing evidence of previous reproductive
205 activity). This latter class includes 'resting' mature females, ovulating females (based on
206 presence of *corpus luteum* and large Graafian follicles), and females that had recently aborted.
207 Distinguishing among these categories was not always possible and they are therefore grouped
208 together. The indicators used to suggest recent abortion rather than dystocia or parturition,
209 include an open cervix, asymmetric uterine horns, and, in particular, gross or histological
210 evidence of lesions or remodelling in the uterine body. In addition, note that very small fetuses

211 are likely to be missed during necropsy so the number of pregnant animals is likely to be
212 underestimated; this bias is taken into account when estimating pregnancy rate (see below).
213
214 *Male reproductive status*
215 During the postmortem examination of males, both testes were removed, weighed (when
216 possible) and preserved in 10% neutral buffered formalin. Where testes were large in size, a
217 cross-section of the mid-testis was collected for fixation and storage. Sections, approximately
218 2×2×0.5 cm, were dissected from the middle of each testis with its associated epididymis, and
219 stored in 70% ethanol before processing for histology. The tissue was dehydrated using 30%,
220 50%, 70%, 80%, and 95% graded ethanol solutions, absolute ethanol, and butanol. The tissue was
221 then embedded in paraffin wax, sectioned at 7 μm, stained with hematoxylin and eosin, and
222 mounted on a glass slide with DPX.
223 The reproductive status of male harbor porpoises was determined based on the mean diameter
224 of the seminiferous tubules, the relative proportion (low, medium, and high) of sertoli cells,
225 interstitial tissue, and germinal cells such as spermatogonia, spermatocytes, spermatids, and
226 spermatozoa. Males were classified as (i) Immature (abundant interstitial tissue and sertoli cells,
227 primary spermatogonia present, diameter of seminiferous tubules <50-60 μm); (ii) Pubescent
228 (reduction in density of interstitial tissue and sertoli cells, some production of spermatocytes,
229 seminiferous tubules ~80 μm); (iii) Active mature (sertoli cells rare, abundant spermatogonia,
230 spermatocytes, spermatids and spermatozoa, epididymis full with spermatozoa and actively
231 secreting epithelium, seminiferous tubules ~200 μm); or (iv) Resting mature (postseason,
232 numerous sertoli cells, few germinal cells or numerous spermatogonia and spermatocytes with

233 some spermatids and spermatozoa in tubules, seminiferous tubules are various sizes) (Hess 1999;
234 Neimanis *et al*. 2000; Murphy *et al*. 2005).
235
236 *Age and length at sexual maturity (ASM and LSM)*
237 The average age and length at attainment of sexual maturity were estimated by fitting binomial
238 GLMs (with logit link function) to data on maturity *vs*. age and maturity *vs*. length, respectively,
239 in both sexes. Age at 50% maturity is given by -*a*/*b* where *a* is the intercept parameter and *b* is
240 the slope. Confidence limits were estimated by bootstrapping (1,000 runs), using the "boot" and
241 "boot.ci" functions (from the boot library) in R (version 2.9.1). Confidence intervals were
242 calculated using the adjusted bootstrap percentile (BCa) method. Binomials GAMs were also
243 fitted to investigate whether there was any significant departure from a standard logistic curve.
244
245 *Pregnancy rate*
246 The pregnancy rate was estimated as the proportion of pregnant females (*i.e*., those with a
247 fetus present) in the sample of mature females. To avoid missing the presence of early embryos,
248 samples from the period of implantation were excluded from this calculation (Read 1990*a;* Read
249 and Hohn 1995). Different sources of evidence from the present study regarding the conception
250 period were not entirely consistent and calculations were therefore made based on each of the
251 plausible alternatives. As a means of checking how much bias might result from missing early
252 embryos, we also repeated the calculations using mature females from the whole year.
253 The 95% confidence limits of the pregnancy rate estimates were obtained based on
254 approximating the binomial distribution with a normal distribution, as justified by the central
255 limit theorem.
256

257 *Reproductive cycle*

258 The reproductive cycle (ovulation, conception, gestation, calving, and lactation periods) of
259 female harbor porpoises in Scottish waters was determined by examining the reproductive status
260 of male and female porpoises, and the body length of fetuses and neonates (see below), in
261 relation to the reported stranding or bycatch date.

262

263 *Gestation period, dates of conception, birth and lactation period*

264 The gestation period was estimated from fetal growth rate and mean length at birth (from the
265 sample of neonates which retained fetal characters), taking into account the initial lag period or
266 nonlinear phase, while individual conception dates were calculated by subtracting the estimated
267 fetal age (t in days) from the date on which the animal was found (Julian date) (after Börjesson
268 and Read, 2003). Fetal age at birth, equivalent to the duration of gestation, is given by:

269 $$\text{Fetal age} = (L_{birth}/u) \times 30.5 + t_0$$

270 where, u is the fetal growth rate (equal to the slope of the linear regression of fetal length (mm)
271 on month), L_{birth} is the mean length at birth (mm), 30.5 is the average days in a month, and t_0 is
272 the estimated duration of the lag phase. The estimate for t_0 uses an equation for eutherian
273 mammals from Calder (1982):

274 $$t_0 = 7.25 \text{ x } (m_{birth}^{0.19})$$

275 where m_{birth} is the mean mass at birth (g).

276 Probable dates of birth for fetuses were estimated from calculated conception dates and
277 gestation period (*i.e.*, assuming that all fetuses have the same growth rate).

278 Lactation period was estimated based on when lactating females were found and from
279 examination of the stomach contents of neonates and calves. We present data on the occurrence
280 of solid food in stomachs of animals up to 110 cm long (a cut-off point identified retrospectively

as the approximate size of 1-yr olds according to fitted growth curves; see below). Length at weaning (*Lw*) was thus estimated based on the size of the smallest calves found with solid food in the stomach and largest animals with milk in the stomach, as well as by applying the Huang *et al*. (2009) equation:

$$Lw = 1.239Lx^{0.877}$$

where, *Lx* is maximum female body length (cm).

Data analysis, exploration and quality control

Data were screened for any implausible combinations of length, age, and maturity and any suspect values were checked against original data, where necessary referring back to the necropsy notes. Transcription errors were corrected and any remaining suspect values were deleted from the subsequent analysis. Except where otherwise stated, data exploration and statistical modelling were performed using Brodgar software (version 2.7.2.) (www.brodgar.com) linked to R (version 2.9.1) or directly in R 2.9.1.

RESULTS

Table 1 summarizes the sample composition used in this study and the data available for 944 harbor porpoises recorded by the SAC in Scotland between 1992 and 2005.

Fetal growth and size of neonates

Fetuses (*n*=18) had body lengths in the range 5.7-88 cm. Fetal lengths in the five dystocia cases for which intact fetuses were recovered (and which thus represent near fullterm fetuses) ranged between 67-78 cm. A linear regression of fetal length on date (treating September as the

305 starting point) provided a reasonably good fit, with month explaining 79.1% of the observed
306 variation in fetus length (Fig. 1). However, a small fetus recorded on 1 May is a clear outlier and
307 excluding this animal, r^2 rises to 89.8% (*n*=17). The slope of the original regression line indicates
308 a fetal growth rate of 80.40 mm/mo; excluding the outlier, fetal growth rate is 84.4 mm/mo.
309 The two smallest stranded animals were 60 cm in length but neither was sent for postmortem
310 so it cannot be confirmed that they were fullterm. The smallest individuals that were necropsied
311 were 65 and 66 cm in length. Excluding the 60 cm animals, therefore, neonates (*n*=78, using a
312 cut-off size of 90 cm) had a minimum body length of 65 cm. Average length and mass were 79.1
313 cm (95% CI=77.6-80.5 cm; *n*=80) and 7.38 kg (95% CI=6.77-7.99 kg; *n*=46) (see Table 2 for
314 further details). It is evident that ≤90 cm individuals occur almost exclusively in May to August
315 (Fig. 1).
316 The small subset (*n*=8) of neonates displaying diagnostic characteristics (*i.e.*, presence of fetal
317 folds and/or hairs still present in bristle pits) ranged in length from 66-84 cm (mean 76.2 cm) and
318 4.6-7.9 kg (mean 6.43 kg). Taking these animals together with the largest fetuses (lengths above
319 66 cm, *n*=6), we estimate average birth length and mass as 76.4 cm and 6.84 kg (Table 2).
320
321 *Postnatal body length, mass and age*
322 Excluding fetuses, body length ranged from 60-175 cm (*n*=861, although as noted above the
323 smallest animals may not have been fullterm) and body mass from 4.5-72.9 kg (*n*=463), with
324 females and males having a similar range of body lengths (Table 2). Body mass was available for
325 19 pregnant females and ranged from 38.0-69.2 kg (54.70±8.04 kg). There was no evidence from
326 the postmortem to suggest that the heaviest female (72.9 kg) was pregnant. Ages of both sexes
327 ranged from <1 yr to 20 yr (*n*=358, Table 2). Seventy-seven animals (22%) were <1 yr old. The
328 majority (approximately 61%) were aged ≤5 yr, with only 7.5% aged 12 yr or older.

329

330 *Growth: length at age*

331 GAM results confirmed that a model with separate smoothers for effects of age on length in
332 males and females was a better fit than one with a common smoother for age (ANOVA, F=4.59,
333 P=0.0047), confirming a sex-related difference in the growth trajectory. In addition, females are
334 significantly longer at age than males (t=5.87, P<0.0001). This model explained 80.1% of
335 deviance in length. Based on separate GAMs for both sexes (Fig. 2), asymptotic length is reached
336 at around age 12 yr. At age 12 yr males have a (fitted) length of 147.2 cm (*SE*=1.66, 95%
337 CI=143.95-150.5 cm) and females aged 12 yr have a length of 158.4 cm (*SE*=2.69, 95%
338 CI=153.1-163.8 cm).

339 The Gompertz curves (Fig. 3) provided a moderately good fit to the length-at-age data for both
340 sexes (r^2=0.810 in males and 0.783 in females). Both curves suggest that physical maturity is
341 reached at around 12 yr, by which age the 95% confidence intervals for fitted length encompass
342 the fitted length at 20 yr old. At 12 yr old, the fitted body length for males is 148.3 cm (95%
343 CI=146.3-150.0 cm) and that for females is 160.7 cm (95% CI=157.7-163.8 cm), *i.e.*, slightly
344 larger than predicted by the GAM fit. At age 20, fitted length for males was 149.7 cm long (95%
345 CI=147-.1-152.3 cm) and that for females was 163.0 cm (95% CI=158.8-167.4 cm).

346 A simple two-stage linear fit (not illustrated) suggested that a switch between positive and
347 zero growth occurred at 5.9 yr (*SE*=0.37) and 145.9 cm (95% CI=140.7-151.2) in males and 5.8
348 yr (*SE*=0.34) and 156.1 cm (95% CI=153.2-159.1) in females. Sums of squares for these fits
349 were slightly lower than for the Gompertz curves and the distributions of residuals were
350 satisfactory.

351

352 *Growth: mass at length*

353 GAMs were also used to investigate length-mass relationships. Results of an *F* test (*F*=4.93,
354 *P*=0.0081) confirmed that the fitted length-mass relationship differed significantly between the
355 sexes. The difference remained significant if pregnant females were excluded (*F*=3.26,
356 *P*=0.0394).
357 The fitted curve for nonpregnant females was somewhat closer to linear (*i.e.*, closer to a
358 simple power curve fit for untransformed data) than that for males (*estimated degrees of freedom*,
359 edf=1.97 for females, 2.41 for males). In males, the slope of the mass-length relationship is
360 reduced at higher lengths. Nonpregnant females were significantly lighter, in relation to their
361 length (*t*=4.12, *P*<0.0001) than males, although the fitted curves suggest that this would not be
362 the case in the very smallest and largest animals (Fig. 4). The separate model for males explained
363 90.7% of deviance, as compared to 91.9% for the model for nonpregnant females.
364 Based on the fitted models, predicted lengths at age 0 were 98.2 cm for males and 99.2 cm for
365 females. These relatively high values reflect the fact that not all "age 0" animals were neonates.
366
367 *Female reproductive status*
368 Reproductive status was determined for 178 female porpoises, of which 76 were mature and
369 102 immature. In addition there were 15 neonate females, which can be assumed to have been
370 immature. Of the mature females, 21 were pregnant (with a fetus present), including two which
371 were pregnant and lactating, while a further 11 were lactating but not pregnant. The remaining 44
372 mature females were neither pregnant nor lactating and classed as resting mature.
373 Ovary masses were available for 90 females. Combined ovary mass (left and right) for
374 immature females (0.88±0.57 g, *n*=58) was, as expected, smaller than that of mature females
375 (5.52±2.23 g, *n*=32) and the highest masses were recorded for the ovaries of pregnant females

(8.27±1.95 g, *n*=6; Table 3). Masses for the left ovaries in both immature and mature females were generally greater than those for the right ovaries (Table 3).

Male reproductive status

Based on histological analysis of samples from 143 male porpoises, reproductive status could be determined for 141 males. Of these males, 55 were classified as mature, 12 pubertal and 74 immature. In addition, four neonate males were assumed to be immature. Fifteen of the 55 mature males were classed as active.

Testis mass (left and right gonads) was available for 35 males (see Table 4 for details). The combined testis masses of immature males (maximum of 84 g, ≤0.25% of body mass) were smaller than those of pubescent and resting mature males (in which combined testis mass ranged between 0.5% and 1.1% of body mass), while active mature males had considerably larger testis masses (a maximum of 3.8 kg combined testis mass, and ranging from 1.3% to 6.8% of body mass. There was not much difference in the left and right testis masses, with the exception of one pubescent male in which the right testis weighed 186g while the left was only 21g.

Age and length at sexual maturity (ASM and LSM)

Seventy-eight (96.3%) of the 81 immature female porpoises with length data were ≤140 cm in length. This included four neonates (66-79 cm length) while the remaining immature animals ranged from 93-148 cm. Ages ranged from <1 yr to 5 yr, with the majority (88%) aged <4 yr old. There were 63 mature females, the majority (95%) being ≥140 cm and 97% aged ≥4 yrs. The smallest mature female was 119 cm long and 3 yr old, which is unusual. Excluding this animal, body lengths of mature females ranged from 137-173 cm and ages from 3.5-20 yr.

399 Immature male porpoises had body lengths from 84-130 cm (n=59) and all but one (5 yr old)
400 were aged ≤3.5 yr. Pubescent males ranged from 119-153 cm and were aged 1-7 yr (n=7). Aside
401 from the youngest (and smallest) animal, which would appear to be unusually precocious, the
402 range was 2-7 yr and 123-153 cm. The active mature male porpoises (n=14) had body lengths
403 between 135-157 cm and were aged 6-15 yr. Resting mature males (n=32) had body lengths
404 between 116-160 cm and ages ranged from 4-20 yr. The two smallest mature males (116 and 126
405 cm) were both 4 yr old.
406 GAM results showed that maturity in both sexes was strongly related to age (P<0.001 in both
407 cases) and fitted smoothers for the effect of age were linear (df=1), justifying the use of GLM for
408 the final models. A binomial GLM (see Table 5 for model parameters) for maturity at age in
409 females (n=144) estimated an ASM of 4.35 yr (95% CI=3.93-4.71, 83.6% of deviance
410 explained). For males, the estimate was 5.00 yr (95% CI=4.03-5.88, 82.3% of deviance
411 explained).
412 LSM was estimated at 138.8 cm (95% CI=135.9-141.6; 79.7% of deviance explained) for
413 females (n=190) and at 132.2 cm (95% CI=129.1-135.6; 69.7% of deviance explained) in males
414 (n=145). Model parameters and standard errors are given in Table 5.
415
416 *Pregnancy rate*
417 Taking the range of conception dates to be 26 May to 14 September, and excluding mature
418 females recorded between these dates to reduce error due to missing early term fetuses, there
419 were 42 mature females of which 17 were pregnant (with a fetus present), giving a pregnancy rate
420 of 0.40 (95% CI=0.26-0.55). Excluding mature females from the entire May to September period
421 leaves 35 mature females of which 13 were pregnant, giving a pregnancy rate of 0.37 (95%
422 CI=0.21-0.53). Taking into account the presence of active mature males from April onwards and

423 therefore excluding mature females from April to September, estimated pregnancy rate 0.34
424 (95% CI=0.17-0.52), based on 29 mature females of which 10 were pregnant. These figures
425 equate to a mature female becoming pregnant on average once every 2.5 to 3 yr. Only two of the
426 21 pregnant females (9.5%) sampled were also lactating, which suggests these porpoises are
427 rarely simultaneously pregnant and lactating.
428 The estimate of pregnancy rate including mature females collected all year round would have
429 been 0.28 (95% CI=0.18-0.38), based on 21 of 76 mature females being pregnant.
430 Unsurprisingly, given the low sample sizes, the considerable overlap in 95% confidence limits
431 indicates that these various estimates are not significantly different.
432
433 *Reproductive cycle*
434 Pregnant females with a fetus (*n*=19) present but not lactating were found between November
435 and June, the two females that were both pregnant and lactating were found in September and
436 November, while lactating (nonpregnant) females (*n*=11) were present during June to November,
437 most (63.64%) being recorded in June and July. Mature females classified as 'resting' (*n*=44)
438 were found in every month, with the highest number (25%) recorded in June.
439 Reproductively active mature males (*n*=15) were recorded from April to July, resting mature
440 males (*n*=40) were recorded in every month, except April and July, while pubescent males (*n*=12)
441 were found between March and June and in September (*n*=1) and October (*n*=1).
442
443 *Gestation period and dates of conception*
444 Based on a mean mass at birth of 6.8 kg (see above), the lag phase of fetal growth would last
445 38.8 d. Based on the smallest confirmed neonate (4.1 kg) and largest fetus (9.5 kg) the lag phase
446 would be 35.2 and 41.3 d respectively. Using the figure of 38.8 d, and applying the higher fetal

447 growth rate calculated previously, gives a gestation period of 314.9 d (10.3 mo), as compared to
448 328.6 d (10.8 mo) if the lower growth rate estimate were used.

449 The seasonal distributions of female reproductive status and of neonate and fetus body lengths
450 are also consistent with a gestation period of around 10-11 mo. Intact fetuses were recorded
451 between September and June, with the smallest fetus recorded in September (5.7 cm) and the
452 largest (88 cm) in May.

453 Similarly, taken together, the seasonal distributions of pregnant females, lactating females and
454 reproductively active males, and neonate and fetus body lengths, suggest that conception usually
455 takes place before September (the smallest fetus, 5.7 cm long, was recorded in September). Back-
456 calculating the date of conception for each fetus by subtracting the estimated fetal age (based on
457 fetal length, and using the higher growth rate estimate) from the date found gives a range of
458 conception dates, from 26 May (for the 88 cm fetus recorded in May 2003) to 14 September (a 51
459 cm fetus recorded in April 2003). However, all but three estimated conceptions (n=17, excluding
460 the previously identified outlier) occurred in July and August, with the mean date of conception
461 calculated as the 4 August (SD=26.6 d). Using the lower growth rate estimate would shift the
462 mean conception date back to 26 July (SD=28.2 d).

463

464 *Calving period*

465 Recent births (n=8) were recorded between 30 May and 27 July, while dystocia cases (n=8)
466 occurred between 16 May and 1 August (all but two in May and June). Furthermore, 73 (91.25%)
467 of the 80 "neonates" (≤90 cm, likely 0-2 mo old) were recorded during May to August, with the
468 majority (n=52; 65%) recorded in June and July (Fig. 1).

469 Estimated dates of birth of the fetuses (n=17, again excluding the outlier), based on estimated
470 dates of conception and gestation period (314.9 d), and the higher fetal growth rate estimate,

471 ranged from 6 April to 26 July, with a mean of 15 June (*SD*=26.6 d). Note that the earliest
472 estimated birth date relates to the largest fetus, which was on 18 May. Excluding this animal
473 shifts the earliest estimated birth date to 22 May and the mean to 20 June. Adopting the slower
474 growth rate estimate (and gestation period of 328.6 d) results in a mean birth date of 20 June (24
475 June if the largest fetus is excluded).
476
477 *Lactation period and weaning*
478 Lactating females (*n*=13) were recorded between June and November. Milk was found in the
479 stomachs of only two neonates, in June and July 2001 (79 and 84 cm respectively). Remains of
480 solid food were found in the stomachs of 41 animals <110 cm long and these were recorded all
481 year round, although predominantly (65%) during February to May. The ten smallest individuals,
482 ranging in length from 86 to 101 cm in length, were recorded during February to September, six
483 of them in February. These smallest animals had eaten mainly whiting (*Merlangius merlangus*),
484 gobies (Gobiidae) or sepiolids (Sepiolidae). Considering all 41 animals <110 cm long, the diet
485 between January and mid-March was dominated numerically by these three prey categories, with
486 small numbers of clupeids, sandeels (Ammodytidae) and other gadoids also recorded. From mid-
487 March to September, sandeels assumed greater importance. For full quantitative details of diet,
488 see Santos *et al.* (2004). We tentatively suggest that weaning occurs mainly from February to
489 May.
490 Using the Huang *et al.* (2009) equation, length at weaning was estimated to be 105.3 cm (95%
491 CI=102.2–108.5 cm) based on the estimated asymptotic body length (158.4 cm, 95% CI=153.1-
492 163.8 cm) or 113.7 cm based on a maximum observed female body length of 173 cm.
493
494

DISCUSSION

As a source of information on biological, reproductive and life history parameters, the 944 harbor porpoises stranded and bycaught over the 14-year study period represent only a small fraction of the extant population, estimated as 385,617 animals (*CV*=0.20, 95% CI=261,266-569,153) in the summer of 2005 for the North Sea and adjacent waters (SCANS-II survey area) (Hammond *et al*. 2013). However, for such a widespread and numerous species there is no realistic possibility of monitoring the living population to derive life history parameters, unlike (for example) the situation with small resident bottlenose dolphin populations (*e.g.*, Grellier *et al*. 2003; Wells *et al*. 2005).

Adult body size

The harbor porpoise is one of the smallest cetaceans and body size varies with geographic location. Porpoises from Scottish waters (1992-2005) have a similar maximum recorded body length (175 cm, *n*=861) to porpoises from Iceland (174 cm, *n*=1266), are slightly larger than animals from West Greenland (166 cm, *n*=176), and smaller than animals from Spain (202 cm, *n*=59), Portugal (202 cm, *n*=37) and indeed smaller than porpoises previously studied around the British Isles (1985-94) (189 cm, *n*=210) (Lockyer 1995*a*, 2003*a*; Sequeira 1996; Lens 1997; Ólafsdóttir *et al*. 2002). Most of the studies cited were based on relatively small sample sizes, with closest agreement being obtained with the study with the largest sample size. Nevertheless, it is apparent that iberian porpoises reach a larger maximum size than those in northern Europe.

Fetal growth and size at birth

The estimated fetal growth rate in porpoises from Scottish waters was approximately 84 mm/mo, which is very similar to the estimated growth rate of 83 mm/mo of porpoises from the

519 Kattegat and Skagerrak Seas, and historic data from the North and Black Seas (Börjesson and
520 Read 2003).

521 The estimated average length at birth (76.4 cm) is also similar to values reported in other
522 studies, including Iceland, Kattegat and Skagerrak Seas and California, although slightly greater
523 than estimates from Denmark and UK (Hohn and Brownell 1990; Sørensen and Kinze 1994;
524 Lockyer 1995*a*; Börjesson and Read 2003; Lockyer and Kinze 2003; Ólafsdóttir *et al.* 2002).
525 There was a wide range of length at birth, which is consistent with the other studies, suggesting
526 that a wide range of birth sizes is usual.

527 In the present study the smallest neonates were 60 cm in length, although it cannot be
528 confirmed that these were fullterm as they were not necropsied. The next smallest animals were
529 65 and 66 cm, while those neonates recorded as displaying fetal characters ranged in length from
530 66 to 84 cm. The largest recorded fetus was 88 cm long although this appears to be exceptional
531 (and if it grew at the average rate it should have been born some 6 wk prior to the date its mother
532 died) and the next largest fetuses were 77-78 cm. However, as noted above, it is possible that the
533 smallest neonate lengths represent premature births and that the largest fetus were abnormally
534 large - several (although not the largest) were associated with maternal mortality due to birth
535 difficulties.

536

537 *Postnatal growth and sexual dimorphism*

538 The fitted Gompertz growth models suggest that physical maturity is not reached until around
539 12 yr for both sexes. However it is apparent from the 2-stage linear fits that a shift from rapid
540 growth to slow or zero growth can be identified at approximately 6 yr in both sexes and the
541 relatively wide variation in size at age in both sexes makes it difficult to identify the age at
542 physical maturity with any certainty. Lockyer (1995*a*) found most porpoises reached a maximum

543 size by the age of around 8 yr in a sample of 234 stranded and bycaught animals from the British
544 Isles between 1985 and 1994, and for female porpoises from the Bay of Fundy the estimated age
545 of physical maturity was 7 yr (Read and Tolley 1997).

546 The Gompertz growth model has been used to describe the growth of several cetacean species,
547 including the harbor porpoise, and appears to provide the best fit for most cetaceans (*e.g.*, Read
548 and Gaskin 1990; Read and Tolley 1997; Stolen *et al*. 2002; Richardson *et al*. 2003). A single
549 Gompertz growth curve was used in the current study, as asymptotic values obtained from this
550 plot were thought to be sufficient for assessing if individuals had attained a stable adult size (after
551 Murphy and Rogan 2006). An improved fit was not obtained using a 2-stage Gompertz curve;
552 indeed a 2-stage linear model was a slightly better fit than the Gompertz model, which likely
553 reflects the high variability in length at age in both sexes. In our study, Gompertz models
554 provided moderately satisfactory fits to the data while the application of GAMs allowed the
555 capture of departures from the growth form assumed by the Gompertz curve.

556 Harbor porpoises are sexually dimorphic, with females being larger than males (Yurick and
557 Gaskin 1987; Gaskin 1984; Read 1999; Lockyer 2003*a*), which was also found in this study. Our
558 results confirm a significant sex-related difference in the growth trajectory, as also reported by
559 many authors (*e.g.,* Gaskin and Blair 1977; van Utrecht 1978; Stuart and Morejohn 1980; Noldus
560 and De Klerk 1984; Read and Gaskin 1990; Read and Tolley 1997; Galatius 2005), with females
561 having faster growth rates than males (*i.e*., they are longer at a given age), while males of a given
562 length are heavier than females. It is thought that female harbor porpoises attain a larger size than
563 males to allow the birth of larger calves, which would have better chance of survival in the cold
564 waters inhabited by harbor porpoises (Stuart and Morejohn 1980; Read and Tolley 1997; Galatius
565 2005). However, as noted above, the largest adult sizes in this species are seen in Spanish and
566 Portuguese Atlantic waters.

567

568 *Age and lifespan*

569 The estimated life expectancy of harbor porpoises in captivity is 43-47 yr, based on brain and
570 body mass regressions (Sacher 1980). In our sample the maximum age recorded was 20 yr, while
571 24 yr was the maximum age recorded by Lockyer (1995*a*) in the UK (1985-94) and in Denmark,
572 with examples of harbor porpoises of more than 20 yr also reported from Iceland and California
573 (Lockyer 2003*a*; Ólafsdóttir *et al*. 2002).

574 The majority of harbor porpoises that have been examined generally have a short life, with
575 most not reaching physical maturity (*e.g*., Lockyer and Kinze 2003), a result also found in our
576 sample, with only 7.5% of porpoises aged ≥12 yr. It is possible that the sampled age (at death)
577 distribution is not fully representative of the porpoise population inhabiting Scottish waters.
578 However, even if this is the case, calculation of most life history parameters (*e.g*., length-at-age,
579 age at sexual maturity), and comparisons between different subsets of porpoises (*e.g*., males *vs*.
580 females) should still be valid.

581

582 *Age of sexual maturity*

583 In early maturing cetacean species, such as harbor porpoises, small changes in age of sexual
584 maturity (and hence first pregnancy) can produce large changes in the rate of population growth
585 (Hohn 1989); therefore ASM is an important criteria in evaluating the status of a population
586 (DeMaster 1978). Age of sexual maturity has been used as an index of the condition of a
587 population or the relative carrying capacity of an area (Eberhardt and Siniff 1977; DeMaster
588 1984; Fowler 1984). For example, higher density populations tend to have a greater average age
589 of sexual maturity (DeMaster 1984).

590 ASM in both female (4.4 yr) and male (5.0 yr) porpoises from Scottish waters were higher
591 than estimates available from other areas, such as Iceland (3.2 and 2.9 yr), Gulf of Maine (3.4 and
592 >3 yr), Denmark (3.6 and 2.9 yr) and West Greenland (3.6 and 2.45 yr for females and males,
593 respectively) (Sørensen and Kinze 1994; Read and Hohn 1995; Lockyer *et al*. 2001, 2003;
594 Ólafsdóttir *et al*. 2002). Geographical differences in ASM could arise for many reasons,
595 including consequences of differences in porpoise population density and/or prey availability or
596 other habitat characteristics. For example, in the Bay of Fundy changes in the age and length at
597 sexual maturity of female porpoises have been observed and are thought to be linked to a
598 decrease in porpoise density caused by incidental mortality in commercial fisheries and/or linked
599 to increased prey availability (Read and Gaskin 1990). However, it is also possible that the
600 estimates of ASM in our study are biased (slightly upwards) due to the high incidence of deaths
601 resulting from poor health (*i.e*., pathological conditions) in the animals sampled (28% of
602 necropsies), in that poor health may delay individual maturation. The majority of porpoises
603 sampled (approximately 61%) had not reached ASM (*i.e*., aged ≤5 yr).
604
605 *Female reproductive status*
606 Female reproductive status was determined based on postmortem findings and histological
607 examination of the ovaries. Combined ovary mass was taken when possible; however, due to the
608 overlap between immature and mature females, it was not found to be a reliable indicator of
609 female reproductive status. All CL present on the ovaries of female porpoises in this study were
610 associated with an actual or recent pregnancy. However, not all CA appear to be derived from CL
611 of pregnancy, as several females had higher numbers of CA than would be expected if they were
612 related to pregnancy, even when taking into account variation in the age of attainment of sexual

613 maturity. CA can result from both the regression of a CL of pregnancy and from an unfertilised
614 ovulation, but there is no clear or definitive method to distinguish between both (Gaskin *et al.*
615 1984, Perrin *et al.* 1984). Therefore, further analysis would be useful to assess the persistence of
616 these scars in porpoises (*cf.*, Dabin *et al.* 2008 for common dolphins).
617
618 *Male reproductive status*
619 Male reproductive status was determined based on histological analysis. However testis mass
620 can also provide a rough indication, as there was a distinct difference in combined testis mass for
621 immature, pubescent and mature males, although some overlap between pubescent and mature
622 resting males.
623 Reproductively active mature males were recorded from April to July while most estimated
624 conception dates for the fetuses recorded were in July or August; a larger sample size might help
625 to illuminate this apparent discrepancy. The distinct seasonal change in male testes may reflect
626 the energetic cost of maintaining large active testes all year (Gaskin *et al*. 1984; Neimanis *et al*.
627 2000). In active mature males from Scottish waters the combined mass of both testes ranged from
628 1.3% to 6.75% of the total body mass. In sperm whales (*Physeter macrocephalus*), the equivalent
629 percentage is only about 0.01%, with little evidence of any seasonal change (Gaskin *et al*. 1984).
630 Greater testis size is generally related with a polygynandrous (promiscuous) mating system (*e.g.*,
631 Perrin and Mesnick 2003).
632 In harbor porpoises, the relative large size of the male testes, sexual dimorphism in which the
633 females are larger, the absence of secondary sexual characteristics, observations of solitary
634 individuals and small group sizes, and no indication of aggressive behavior between males (such
635 as the absence of scarring) all suggests sperm competition plays a major role in the mating
636 system (Fontaine and Barrette 1997; Read and Tolley 1997).

637

638 *Pregnancy rate and senescence*

639 The estimated pregnancy rate determined in our study (0.34-0.40) is equivalent to mature
640 females becoming pregnant, on average, once every 2.5 to 3 yr and is substantially lower than
641 estimates for Denmark (0.73), Bay of Fundy (0.74), Gulf of Maine (0.93) or Iceland (0.98) (Read
642 1990*a*; Sørensen and Kinze 1994; Read and Hohn 1995; Ólafsdóttir *et al.* 2002), all of which
643 were based on bycaught porpoises. The presence of two pregnant and lactating females in our
644 sample, suggest that porpoises in Scottish waters can give birth annually. An annual breeding
645 cycle has been reported for porpoises in the Bay of Fundy, Baltic Sea, West Greenland, and
646 Iceland (Møhl-Hansen 1954; Gaskin *et al.* 1984; Lockyer *et al.* 2003; Ólafsdóttir *et al.* 2002).

647 Many factors could contribute to differences in pregnancy rates, including differences in age at
648 sexual maturity, general health, nutritional condition, the quality and quantity of available food
649 and exposure to contaminants (such as endocrine disrupting chemicals, *e.g.*, Aguilar *et al.* 1999).
650 PCB concentrations recorded in the blubber of female porpoises from Scotland during 2001-03
651 were above the threshold at which effects on reproduction might be expected in almost 40% of
652 individuals (Pierce *et al.* 2008).

653 It is likely, however, that our figure of 0.34 to 0.40 is an underestimate. The present study was
654 based mainly on stranded animals (94.6%), among which there were relatively few mature
655 females sampled outside the implantation period when small foetuses could be missed (between
656 29 and 42 animals depending on how the implantation period is estimated). Of these mature
657 females, around two-thirds were diagnosed as having died from health-related causes (*i.e.*,
658 pathological conditions, such as disease, parasitism, *etc*.).

659 Cause of death was established for 14 of the pregnant females (n=21), five of which had died
660 due to poor health / pathological conditions and five due to dystocia. There were also three

661 additional records of dystocia, one in which the fetus was recorded as “macerating” and two in
662 which no evidence of a fetus was found; these animals were therefore not recorded as pregnant.
663 These findings highlight two potential issues: firstly, the birth rate will be lower than the
664 pregnancy rate, due to abortions and deaths of pregnant females. Secondly, strandings include a
665 high proportion of animals which were to varying degrees suffering from poor health and less
666 healthy females may have both lower pregnancy rates and a lower incidence of successful
667 pregnancies than healthy mature females. Thus pregnancy rate is likely to be underestimated
668 from stranded animals.

669 Senescence, expressed as a substantial age-related decline in fecundity, has been identified in
670 several odontocete species (Perrin *et al.* 1984; Marsh and Kasuya 1984, 1986; Myrick *et al.* 1986;
671 Chivers 2002). Senescence seems not to be documented for (the relatively short-lived) harbor
672 porpoise, although Ólafsdóttir *et al.* (2002) speculated that the single nonpregnant mature female
673 sampled in Iceland, which was 17 years old, may have been senescent. Although the number of
674 older female porpoises recorded in the present study was small, two pregnant females were aged
675 15 yr, and the oldest female in the study (aged 20 yr) showed possible evidence of a recent
676 pregnancy. Thus, there was no indication of senescence in female harbor porpoises from Scottish
677 waters. Similarly, Read (1990*a*) found no evidence of reproductive senescence or declining
678 fertility with age in female harbor porpoises from the Bay of Fundy.

679

680 *Reproductive seasonality and cycle*

681 There is a distinct reproductive seasonality in the harbor porpoise (Read and Hohn 1995;
682 Börjesson and Read 2003). There can be several selective advantages to seasonal reproduction.
683 For example, if food availability is seasonal, as generally occurs at higher latitudes, then females
684 may time the reproductive season so that periods of high energetic demands, such as early

685 lactation, coincide with periods of high prey availability. Other considerations include ensuring
686 the availability of suitable prey at the time of weaning and ensuring that calves are born when
687 water temperatures are warmer and the weather is calmer to increase survival and/or reduce
688 energy expenditure (Whitehead and Mann 2000). In addition, the timing of conception may relate
689 to factors such as the nutritional condition and health of a female (Sørensen and Kinze 1994).
690 In the present study, all active mature males were sampled between the months April and July.
691 Although the occurrence of reproductively active males suggests that conceptions could occur as
692 early as April, estimated conception dates were mainly in July and August, which is similar to
693 results for several other areas of the North Atlantic (Hohn and Brownell 1990; Read 1990*b*;
694 Sørensen and Kinze 1994; Bandomir-Krischack 1996). The lack of samples of active males from
695 August could reflect a sampling bias as healthy active mature males, like healthy pregnant
696 females, may be underrepresented in strandings. The timing of conception in porpoises is
697 thought to relate to the annual photoperiod cycle, which could act as a rough cue to predict the
698 optimal time to give birth (Sørensen and Kinze 1994). Gestation period would not be expected to
699 vary greatly between individuals or areas and the gestation period of harbor porpoises in Scottish
700 waters (10-11 mo) is consistent with published estimates from other studies, which range from 10
701 to 12 mo (Møhl-Hansen 1954; van Utrecht 1978; Read 1990*b*; Sørensen and Kinze 1994;
702 Bandomir-Krischack 1996; Börjesson and Read 2003). In Scottish waters calving probably
703 mainly takes place between May and July, when sea temperatures are increasing, again similar to
704 results from other studies in Europe and North America (Møhl-Hansen 1954; van Utrecht 1978;
705 Hohn and Brownell 1990; Read 1990*b*; Sørensen and Kinze 1994; Bandomir-Krischack 1996;
706 Börjesson and Read 2003).
707 Several cetacean species show variation in the lactation period and weaning age/size, between
708 populations and between individuals (Whitehead and Mann 2000; Evans and Stirling 2001). The

709 length of lactation and size at weaning can significantly affect calf survival, have serious
710 implications for the health of the mother and, therefore, potentially, long-term viability of a
711 population.

712 Based on the available evidence it is not possible to determine the duration of the lactation
713 period with any great certainty. Lactating females were found only during June to November;
714 neonates with milk in the stomach were found only in June and July while evidence of very small
715 porpoises feeding on solid food was evident mainly from February onwards. Estimates of 8-9 mo
716 have been obtained from other areas (Møhl-Hansen 1954; Read 1990*b*; Sørensen and Kinze
717 1994). Weaning in harbor porpoises is thought to start at an age of around 8 mo, although calves
718 may not feed entirely independently until about 10 mo old (Lockyer 2003*a*). Visual identification
719 of milk in the digestive tract is possible only if death happened very soon (<3-4 h) after feeding.
720 After that, the milk is likely to resemble normal gut fluid contents. A possible solution would be
721 to use an assay for milk sugars in gut contents.

722 Applying the Huang *et al.* (2009) method to the maximum female size recorded in the present
723 study, length at weaning was estimated to be 113.7 cm, similar to estimates of 115.1 cm by
724 Huang *et al*. (2009) and 114.7 cm (Lockyer *et al*. 2001). However, if we used the estimated
725 asymptotic size of females, the estimated size at weaning would be reduced to 105.3 cm. In fact,
726 solid food was present in stomachs of some individuals from 86 cm in length upwards.

727 While some calves evidently start to take solid food as early as February, the timing of
728 weaning of the majority of harbor porpoises in Scottish waters (March through May) coincides
729 with the availability of sandeels, an important and relatively energy-rich major component of
730 porpoise diet during the second and third quarters of the year in Scotland (Santos *et al.* 2004).
731 Diet of the smallest individuals generally showed a similar seasonality to that previously
732 described for the whole dataset (to 2003) in Santos *et al.* (2004), with sandeels assuming

733 prominence from mid-March through to September, the other main prey categories being
734 whiting, gobies and sepiolids.
735
736 *Stranding data: sampling biases and value*
737 Previous estimates of life history parameters of harbor porpoises have been variously based on
738 material from directed lethal sampling, fishery bycatches, and strandings, all of which can
739 involve some biases. Strandings, for example, may be biased towards very young, sick, and (to a
740 lesser extent) very old animals (*i.e*., they are representative of the age structure of deaths rather
741 than the age structure of the living population) and towards animals living in coastal waters.
742 However, most "Scottish" porpoises are found relatively close to the coast: in July 1994 the
743 SCANS survey identified two major concentrations of porpoise abundance in the North Sea,
744 along the Danish coast and along the coasts of Scotland and northern England. In 2005, although
745 the highest densities of animals were seen off the east coast of southern England, and there also
746 seemed to be a lower density immediately adjacent to the coast, most animals were seen within
747 around 100 miles of the coast (see Hammond *et al.* 2013). Strandings data in general will also be
748 influenced by carcass buoyancy (dead porpoises seem to float quite well; A. Brownlow Pers.
749 Obs.) and the drift process (affected by prevailing currents), and biased towards those animals
750 notable enough for the public to report (*e.g.* Peltier *et al.* 2013).
751 Different biases may apply to bycatch, the incidence of which may reflect a complex
752 combination of seasonal changes in cetacean and fisheries distributions as well as behavioral
753 processes that can vary with age, sex and reproductive status (Donovan and Bjørge 1995;
754 Lockyer 2003*a, b*).
755 Where possible, the potential biases and limitations associated with using stranded animals in
756 this study have been addressed. However, this has not always been possible, for example, a

757 probable source of bias in this data set is that unhealthy animals may be less likely to become
758 pregnant than those with good health status.

759 The fact that only around a third of strandings yielded age and reproductive status data reflects
760 the fact that necropsies were usually not carried out for animals which were in a poor state of
761 preservation, as well as logistic (*e.g.* related to transport) and financial constraints. It should be
762 noted that teeth could normally be extracted even from badly decomposed animals and collection
763 and analysis of such samples would significantly enhance the data available in future.

764 Despite possible limitations, data from stranded and bycaught animals remain a valuable
765 source of biological and life history information and this long-term study of a large and varied
766 (*i.e.*, ages and times of year for both males and females) sample set, where porpoises had died
767 from different causes (including bycatch, attacks from *Tursiops truncatus*, live stranding and
768 various pathological conditions) offered a unique opportunity to determine the biological and life
769 history parameters of harbor porpoises in Scottish waters.

770 The value of data available from strandings is gaining increasing recognition, for example in
771 relation to patterns of species richness and relative abundance (Pyenson 2011). The establishment
772 of monitoring strategies for small cetaceans is needed under various international agreements and
773 directives (such as ASCOBANS and the European Union's Marine Strategy Framework
774 Directive). In this context, cetacean stranding data have an important role to play, notably
775 because stranded cetaceans constitute the main source of biological material on which vital rates
776 can be estimated, potentially providing early warning of changes in population size. Alternative
777 methods such as photo-identification and serial dedicated surveys also have their limitations and
778 biases. Consequently monitoring strategies will have to rely on several complementary methods
779 and data sources.

780 While the second UK report on implementation of the EU Habitats Directive assessed the
781 conservation status of harbor porpoise in UK waters as favorable (with medium confidence)
782 (Joint Nature Conservation Committee 2007), surveys indicate a southward shift in summer
783 distribution in the North Sea between 1994 and 2005 (Hammond *et al.* 2013). In addition, several
784 of the recorded causes of porpoise mortality in Scotland (disease, starvation, bottlenose dolphin
785 attacks, fishery bycatch) represent potential future threats at population level and high
786 concentrations of POPs have been recorded in porpoises in the northeast Atlantic (*e.g.* Pierce *et*
787 *al.* 2008; Law *et al.* 2010). To assess and model the impacts of any of these threats, we need to
788 know the rate at which the population will grow in the absence of the threat (Stenson 2003). This
789 depends on parameters such as age at sexual maturity and age-specific mortality and birth rates,
790 which can be derived from life history studies. Changes in any of these parameters will affect
791 population growth and, hence, impact on abundance (for example, DeMaster 1978; Fowler 1984;
792 Winship *et al*. 2007; Murphy *et al*. 2009). Use of life history data from strandings monitoring
793 clearly presents challenges, not least to quantify and understand the nature of biases. However,
794 we argue that such data represent an important and arguably undervalued resource.
795
796
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FIGURE LEGENDS

Figure 1. Lengths of fetuses (filled diamonds), confirmed neonates (filled circles), neonates (length ≤90 cm; open triangles) and other animals up to 130 cm (filled triangles) *vs.* date for harbor porpoises from Scottish waters (1992-2005). September is treated as month 1. The regression line fitted to fetal length data excludes the outlier (31 cm fetus from 1 May, shown as open diamond). Note that some lengths of larger animals were estimated.

Figure 2. Length at age curves based on predictions from GAMs for male and female harbor porpoises from Scotland, with 95% confidence limits on the predictions.

Figure 3. Age at length for male and female harbor porpoises from Scotland, with fitted Gompertz curves (with upper and lower 95% confidence limits).

Figure 4. Mass at length curves based on predictions from GAMs (fitted to log-transformed data) for male and female harbor porpoises from Scotland.

1103 **TABLES**

1104

1105 **Table 1.** *Sample composition and data available for stranded and bycaught harbor porpoises*
1106 *around Scotland (1992-2005)*
1107

Sample	***Females***	***Males***	***Unknown sex***	***Total***
All stranded & bycaught porpoises	294	324	326	944
Location				
- east coast	165	196	170	531
- north coast	35	38	36	109
- west coast	91	92	118	301
Necropsy	266	276	3	545
Cause of Death				
- pathological condition	86	66	0	152
- live stranding	3	5	0	8
- physical trauma	5	6	0	11
- dolphin attack	76	87	1	164
- bycatch	14	37	0	51
- starvation	24	18	0	42
- starvation (neonate)	20	14	0	34
- stillborn	3	3	0	6
- dystocia	8			8
- not established	27	40	2	69
Length data	289	320	252	861
Mass data	222	241	0	463
Age data	170	176	12	358
Reproductive status data	178	143	-	321
Reproductive status & age data	144	112	-	256
Fetuses	8	10	0	18
Neonates	26	28	26	80

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Table 2. *Range, sample sizes (n), mean and standard deviation (SD) for body length, mass and age of stranded and bycaught harbor porpoises around Scotland (*nonpregnant females). Females > 158 cm and males > 147 cm are those that have reached asymptotic length (see Results). "Recent births" are those animals in which fetal folds and/or hairs in bristle pits were evident. The combined category "Recent births and largest foetuses" represents our best estimate of size at birth. The category "Animals ≤90 cm" length comprises all newborn and young animals within the previously reported cutoff length for neonates.*

Sample	***Length(cm)***		***Mass (kg)***		***Age(yr)***	
	Range (n)	***Mean (SD)***	***Range (n)***	***Mean (SD)***	***Range (n)***	***Mean (SD)***
All (excluding fetuses)	60-175 (861)	-	4.5-72.9 (463)	-	<1-20 (358)	-
Females	66-173 (289)	127.73 (25.84)	4.6-72.9 (222)	30.84 (16.15)	<1-20 (170)	4.33 (3.93)
Females >158 cm	158-173 (43)	164.21 (4.18)	33.5-72.9 (27)*	51.45 (8.55)*	4-20 (31)	8.98 (3.77)
Males	65-170 (320)	124.11 (22.69)	4.5-61.2 (241)	30.06 (14.55)	<1-20 (176)	4.97 (4.48)
Males >147 cm	147-170 (58)	153.55 (4.60)	31.0-61.2 (43)	45.98 (6.19)	5-16 (34)	9.32 (2.86)
Fetuses	5.7-88 (18)	50.62 (22.92)	08-9.5 (16)	3.85 (3.11)	-	-
Recent births	66-84 (8)	76.2 (5.5)	4.6-7.9 (8)	6.43 (1.13)	-	-
Recent births +_ largest fetuses	66-88 (14)	76.4 (5.9)	4.1-9.5 (14)	6.84 (1.59)	-	-
Animals ≤90 cm	65-90 (78)	79.05 (6.35)	4.5-12.8 (46)	7.38 (2.06)	-	-

1121 **Table 3.** *Ovary mass (range, mean and standard deviation) for stranded and bycaught female*

1122 *harbor porpoises around Scotland (1992 and 2005)*

1123

Females	***Ovary mass (g)***		
	Left	***Right***	***Combined***
Immature (*n*=58)	0.17-1.78 0.47±0.30	0.10-1.24 0.41±0.23	0.30-3.02 0.88±0.52
Mature (*n*=31)	0.95-8.27 4.08±1.86	0.43-3.35 1.44±0.68	1.37-10.39 5.51±2.26
Resting mature (*n*=20)	0.95-6.16 3.53±1.51	0.43-3.35 1.29±0.64	1.37-8.70 4.82±2.00
Pregnant (*n*=6)	4.00-8.27 6.44±1.78	0.95-2.80 1.83±0.72	5.61-10.39 8.27±1.95
Lactating & recently pregnant (*n*=5)	2.07-4.47 3.54±0.92	0.96-2.73 1.54±0.69	4.32-5.93 4.99±0.70

1124

1125

1126 **Table 4.** Testis *mass (range, mean and standard deviation) for stranded and bycaught male*

1127 *harbor porpoises around Scotland (1992 and 2005)*

1128

Males	***Testis mass (g)***		
	Left	***Right***	***Combined***
Immature (*n*=20)	7-44 14.30±10.34	6-40 13.15±8.50	13-84 27.45±18.78
Pubescent (*n*=3)	21-175 122.67±88.06	155-186 171.33±15.57	207-348 294.00±76.07
Active mature (*n*=4)	299-1925 1103.50±704.57	296-1889 1022.00±671.96	595-3814 2125.50±1372.19
Resting mature (*n*=8)	132-290 230.13±51.79	121-290 197.63±55.39	253-580 427.75±99.25

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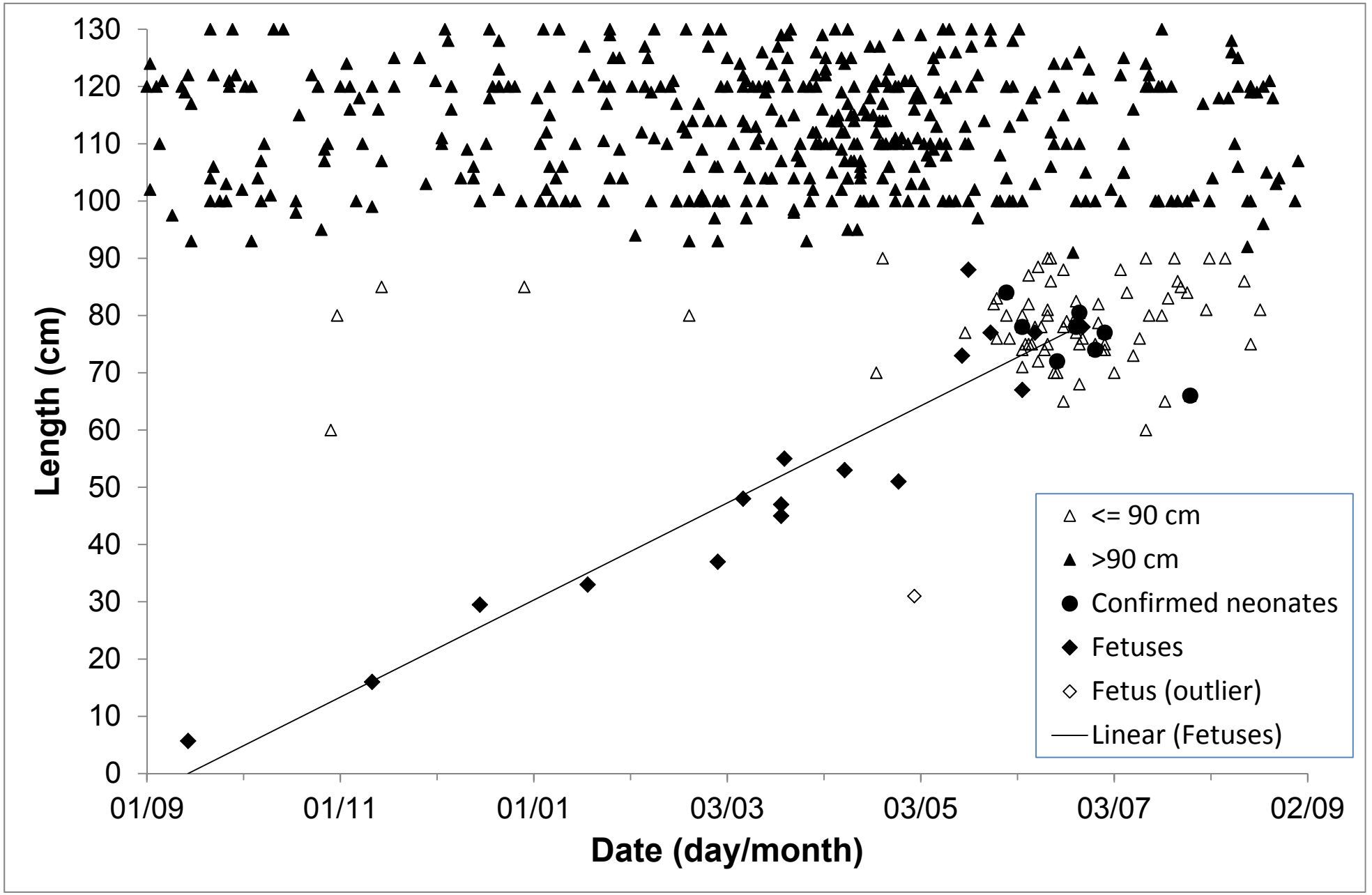
1133 **Table 5.** *Coefficient values (mean with standard error in parentheses) for binomial GLM fits for*

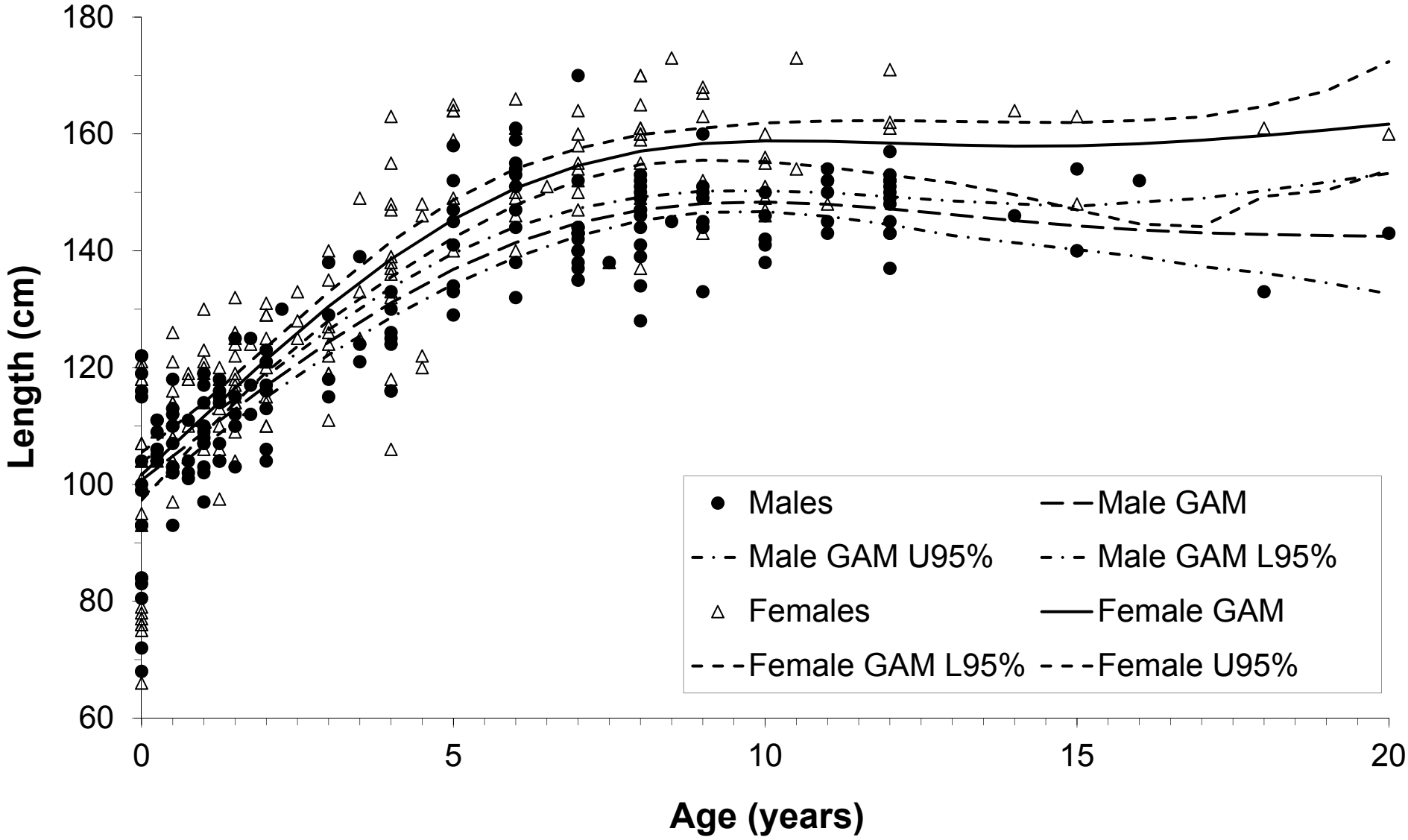
1134 *age and length at 50% maturity. Deviance explained and sample sizes are also given.*

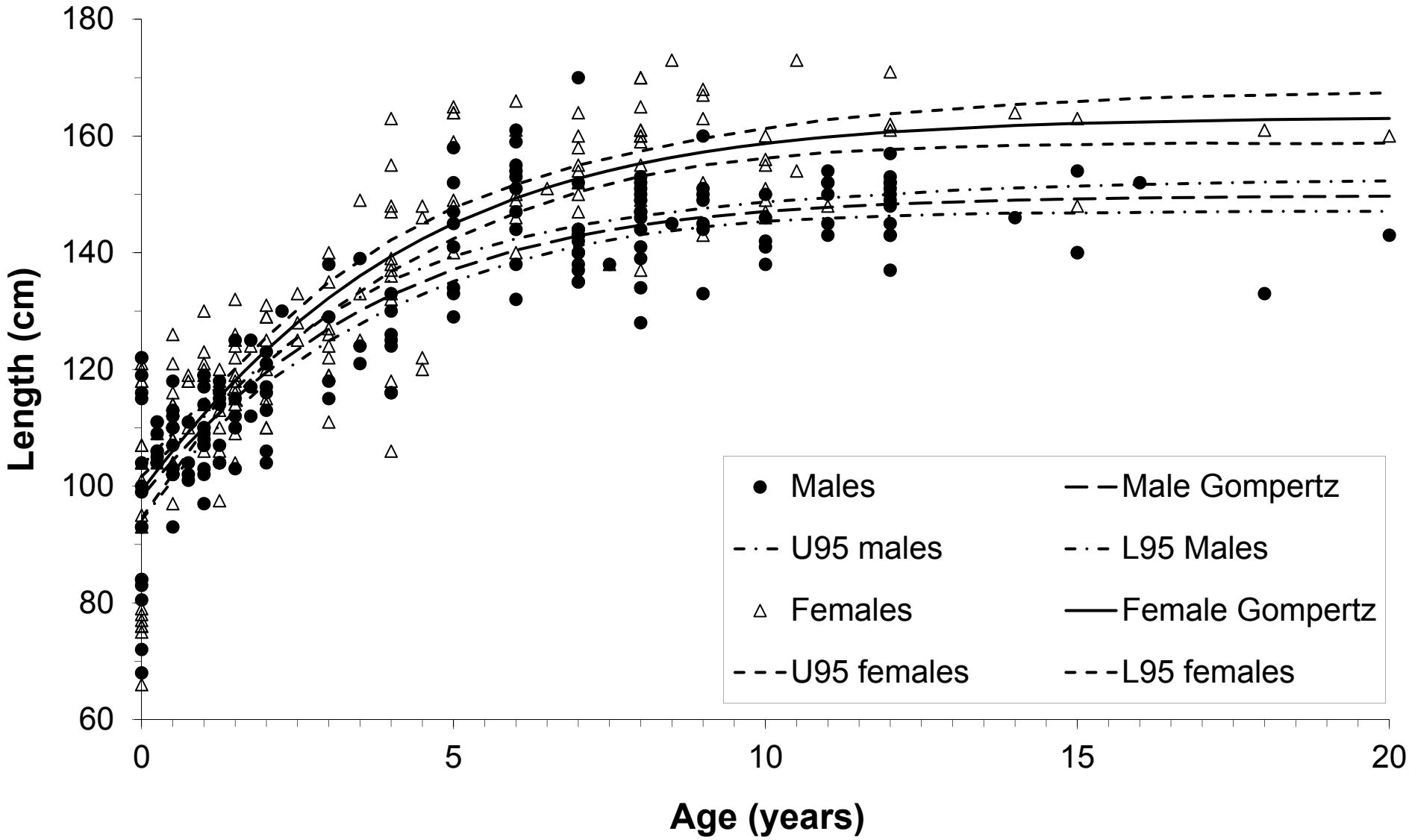
1135

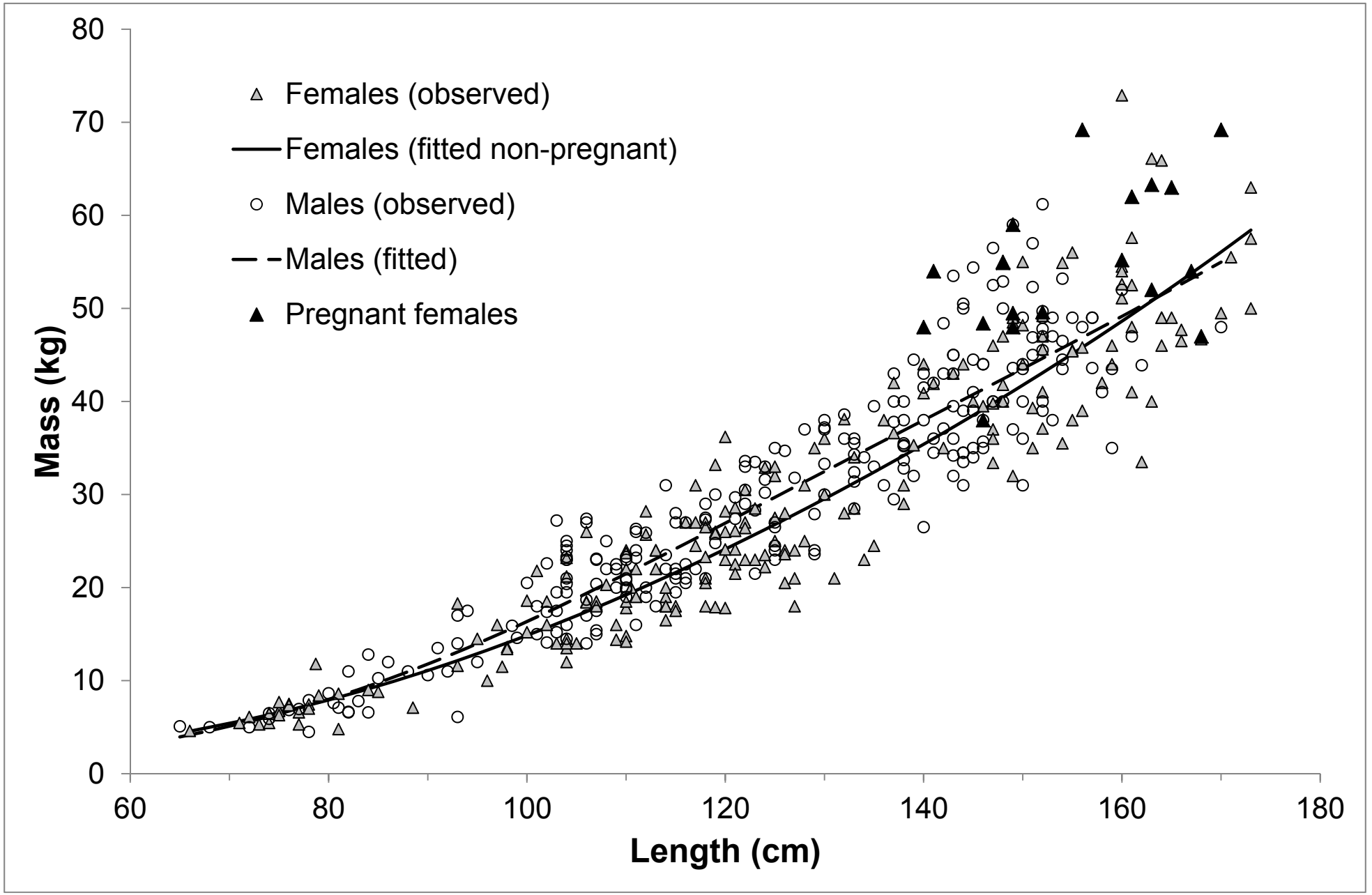
Model	Intercept coefficient	Age or length coefficient	Deviance explained (and sample size)
Age (females)	-9.3615 (2.3334)	2.1544 (0.541)	0.836 (144)
Age (males)	-6.3602 (1.5465)	1.2728 (0.2894)	0.823 (115)
Length (females)	-33.6385 (5.8790)	0.2423 (0.0419)	0.797 (190)
Length (males)	-26.1822 (4.4001)	0.1980 (0.0331)	0.697 (145)

1136


130
120
110
100
90
80
70
60
50
40
30
20
10
0
Length (cm)
01/09
01/11
01/01
03/03
03/05
03/07
02/09
Date (day/month)
<= 90 cm
>90 cm
Confirmed neonates
Fetuses
Fetus (outlier)
Linear (Fetuses)


180
160
140
120
100
80
60
Length (cm)
0
5
10
15
20
Age (years)
Males
Male GAM
Male GAM U95%
Male GAM L95%
Females
Female GAM
Female GAM L95%
Female U95%


180
160
140
120
100
80
60
Length (cm)
0
5
10
15
20
Age (years)
Males
Female Gompertz
U95 males
L95 Males
Females
Male Gompertz
U95 females
L95 females


Females (observed)
Females (fitted non-pregnant)
Males (observed)
Males (fitted)
Pregnant females
Mass (kg)
Length (cm)
0
10
20
30
40
50
60
70
80
60
80
100
120
140
160
180